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VARIATION INTRA-POPULATION DU MOUVEMENT CHEZ L'ESTURGEON JAUNE EN MILIEU LOTIQUE

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AVANT-PROPOS

Cette recherche découle d'un projet initié par le département de ressources naturelles de la communauté anishinabe de Kitigan Zibi (KZA) dans le but de protéger l'esturgeon jaune sur le territoire traditionnel de la communauté.

Ce mémoire se divise en deux chapitres. Le premier chapitre est un résumé substantiel en français d'un manuscrit qui sera soumis au journal *Freshwater Biology*. Le deuxième chapitre est ledit manuscrit en anglais.

RÉSUMÉ

La migration est un aspect fondamental du comportement animal pouvant influencer la dynamique et l'utilisation spatiale des populations et orchestrer des interactions à l'échelle d'écosystèmes. Ainsi, étudier la migration peut procurer une meilleure compréhension des variations dans la distribution et les structures des populations animales. Le phénomène de la migration partielle, lequel se définit par la présence d'individus résidents et migrateurs dans une même population, est considéré le type de migration dominant dans la nature. Comprendre les variations spatiotemporelles et intra-population affectant la distribution des populations animales est important pour l'élaboration et l'implémentation des stratégies de gestion et de conservation.

Dans la présente étude, nous avons suivi les mouvements saisonniers de 26 esturgeons jaunes (*Acipenser fulvescens*) dans un réseau de rivières du sud du Québec. Les esturgeons ont été capturés et marqués d'émetteurs radio internes entre mai 2006 et avril 2010, et ont été suivis par télémétrie active jusqu'à la fin de novembre 2010.

Nous avons utilisé l'analyse des correspondances pour évaluer : 1) l'association des localisations individuelles des esturgeons avec trois secteurs de rivière et 2) l'association temporelle entre les localisations en fonction de deux groupes distincts et les trois secteurs de rivière. Pour déterminer si des variables environnementales (photopériode, niveau de l'eau et température) avaient une influence sur les mouvements saisonniers entre les habitats d'hivernage et d'été, nous avons utilisé un modèle markovien à deux états avec covariables temporellement dépendantes.

Nous avons trouvé que les déplacements individuels étaient globalement cohérents entre les années. Tous les esturgeons suivis pouvaient être classés selon deux patrons de migration, caractérisés par des sites d'hivernage collectifs et des déplacements saisonniers restreints ou sur une longue distance. Les variables environnementales semblaient diriger les déplacements saisonniers, mais avaient une influence différente entre les deux groupes de migrateurs. La redondance interannuelle des patrons de migration individuels et la réponse différentielle aux déclencheurs environnementaux par les deux types de migrateurs démontrent l'occurrence de la migration partielle chez l'esturgeon jaune, et suggèrent que les comportements de mouvements individuels peuvent jouer un rôle important dans le maintien des structures de populations sur une période étendue. Nous élaborons sur l'hypothèse que cette migration partielle est le fruit d'une imprégnation en bas âge jumelé d'un comportement de retour à des sites connus (angl. homing) et discutons des implications de nos découvertes en matière de stratégies de gestion et conservation de la faune.

Mots-clés : *Acipenser fulvescens,* effets environnementaux, hétérogénéité des populations, modèle markovien, migration partielle

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CHAPITRE I

VARIATION INTRA-POPULATION ET DÉCLENCHEURS ABIOTIQUES DES MOUVEMENTS SAISONNIERS CHEZ UNE POPULATION LOTIQUE DE L'ESTURGEON JAUNE

Introduction

Le mouvement est une caractéristique fondamentale du comportement animal pouvant définir le sort des individus, influencer la dynamique et la structure des populations et orchestrer des interactions à l'échelle des écosystèmes (Dingle & Drake 2007; Chapman *et al.* 2011b; Holdo *et al.* 2011). La migration est la forme de mouvement utilisée par plusieurs animaux pour faire face à la variabilité temporelle de leurs besoins et de l'emplacement des ressources (Dingle & Drake 2007; Beyer *et al.* 2010); la migration vers un habitat alternatif augmente ultimement le fitness des individus en donnant accès à la ressource requise (Leggett 1977; Northcote 1978; Dingle & Drake 2007). Toutefois, la migration vient aussi avec des coûts et les individus doivent décider de quelle stratégie – migrer ou rester sur place – offre les meilleurs compromis entre coûts et bénéfices (Brodersen *et al.* 2008b). Puisque cette décision est prise par des individus d'une population, il en découle une variation intrapopulation pouvant mener à la coexistence d'individus résidents et migrateurs, un phénomène appelé la migration partielle (Jonsson & Jonsson 1993; Kaitala *et al.* 1993; Chapman *et al.* 2011b).

La migration partielle est considérée comme le type de migration dominant dans la nature (Lundberg 1988; Jonsson & Jonsson 1993; White *et al.* 2007; Chapman *et al.* 2011b; Grayson *et al.* 2011). Chez les poissons, le phénomène a été documenté pour une variété de contextes écologiques tels que les migrations saisonnières motivées par le compromis entre l'accès à plus de nourriture et l'évitement de la prédation (Brodersen *et al.* 2008), la migration verticale partielle journalière (Mehner & Kasprzak 2011), des stratégies alternatives de cycles biologiques (Kerr *et al.* 2009; Swanson *et al.* 2010) et la

migration entre les habitats d'hivernage et de fraie chez les espèces monocycliques comme polycycliques (Shaw & Levin 2011). Étant donné la diversité de formes que la migration partielle peut prendre et l'étendue des conséquences que cette diversité entraîne (Chapman *et al.* 2011b), il est utile d'étudier les patrons de mouvements au niveau de l'individu afin de mieux comprendre le phénomène et les enjeux (Brodersen *et al.* 2008b; Kerr *et al.* 2009).

Pour l'individu, la migration comprend deux composantes décisionnelles fondamentales, assujetties à des influences extrinsèques et intrinsèques : *quand partir* et *où aller* (Bauer *et al.* 2011). D'abord, pour savoir *quand partir,* les animaux utilisent différentes combinaisons d'indicateurs environnementaux et internes; la température de l'eau, le débit des cours d'eau et la photopériode sont des indicateurs environnementaux qui influencent la migration chez plusieurs espèces de poissons (p. ex., Jonsson 1991; Trépanier *et al.* 1996; Rusak and Mosindy 1997) et les indicateurs internes incluent le stade de développement et l'état physiologique (Trépanier *et al.* 1996; Hunter *et al.* 2009; Bauer *et al.* 2011). Deuxièmement, *où aller* peut être influencé par la génétique (Biebach 1983), l'apprentissage social (Dodson 1988) et la mémoire à long terme (Van Moorter *et al.* 2009).

L'esturgeon jaune (*Acipenser fulvescens*) est une espèce longévive et polycyclique; les mâles fraient pour la premièrement fois vers l'âge de 12-15 ans puis à intervalles de 1-3 ans et les femelles peuvent mettre de 18-27 ans avant le premier frai, puis fraient à intervalles de 3-9 ans (Peterson *et al.* 2007). Les individus matures dans une population, y compris ceux d'une même cohorte, peuvent êtres migrateurs ou résidents en raison de différences individuelles et intersexuelles dans la maturation des gamètes (Auer *et al.* 1996a; Peterson *et al.* 2007). L'esturgeon jaune est typiquement un habitant des environnements lacustres ou de grandes rivières et migre généralement dans de plus petits cours d'eau seulement pour le frai (Auer *et al.* 1996a; Peterson *et al.* 2007). Peu de choses sont connues des mouvements saisonniers des populations d'esturgeon jaune résidant à l'année dans des réseaux de petites rivières sans accès à ces vastes habitats lacustres ou fluviaux (mais voir Rusak & Mosindy 1997; Borkholder *et al.* 2002; Knights *et al.* 2002).

Méthodes

Aire d'étude

L'aire d'étude est un réseau hétérogène de petites à moyennes rivières, centré sur la réserve de la Nation algonquine anishinabe de Kitigan Zibi (N46°20' W75°58'), située dans les plaines alluviales de la vallée de la rivière Gatineau (Québec, Canada). À l'étiage, le réseau représente tout près de 7.24 km^2 d'habitat continu accessible aux esturgeons adultes, sur plus de 106 km des rivières Gatineau, Désert et de l'Aigle, ainsi que de courtes sections de la rivière Hibou et du ruisseau Bitobi (Fig. 2.1). Dans son ensemble, le réseau est un assemblage d'habitats comprenant des fosses profondes (jusqu'à 30 m de profondeur; rivière Gatineau) procurant de l'habitat d'hivernage pour l'esturgeon jaune, des segments méandreux jonchés de gros débris ligneux avec des alternances de fosses et hauts fonds, des chutes, rapides et radiers de gradients variés.

Capture des poissons et télémétrie

Un total de 26 esturgeons adultes variant de 970 à 1460 mm (longueur totale) ont été capturés au moyen de filets maillants dans les rivières Hibou, de l'Aigle et Désert entre mai 2006 et avril 2010, et marqués individuellement par insertion chirurgicale d'émetteurs radio internes selon la méthode de Ross et Kleiner (1982). Avant la chirurgie, les poissons étaient anesthésiés (stade IV; Summerfelt & Smith 1990) par immersion dans une solution d'huile de clous de girofle (60 mg l^{-1}; Peake 1998), pesés et mesurés (longueur totale et à la fourche). Lorsque possible, le sexe était déterminé par l'examen des gonades au moment de la chirurgie. Après la chirurgie, les poissons étaient gardés sous observation jusqu'à ce qu'ils aient récupéré de l'anesthésie (Summerfelt & Smith 1990), puis relâchés au site de capture. Les chirurgies se sont bien déroulées et aucune mortalité ne leur a été attribuée. Le ratio poids de l'émetteur sur poids du poisson était toujours inférieur à 2 %, tel que recommandé par Winter (1996).

Les mouvements des esturgeons ont été suivis par télémétrie radio sur une base bi-hebdomadaire à mensuelle entre mai 2006 et novembre 2010. Les localisations étaient

généralement faites par bateau à moteur, mais aussi par canot ou de la berge lorsque les caractéristiques locales ne permettaient pas l'utilisation d'un bateau à moteur. Les localisations étaient faites au moyen de récepteurs manuels (modèles SRX400 ou Biotracker, Lotek Engineering Systems, Newmarket, ON, Canada; et R410 Scanning eceiver, Advanced Telemetry Systems, Isanti, MN, É.-U.) et d'une antenne Yagi à trois éléments. Pour chaque localisation, les coordonnées, la profondeur et la température de l'eau étaient notées.

Traitement des données

Toutes les localisations d'esturgeons ont été projetées sur une couche SIG de l'aire d'étude pour évaluer les patrons de distribution spatiale intra et inter-individus. Une ligne médiane de rivière a été tracée en une couche SIG et calibrée en kilomètres de rivière (rkm) à partir du rapide St-Joseph à l'extrême nord de la rivière Gatineau (rkm 0.00). Une valeur de rkm a ensuite été assignée à chaque localisation d'esturgeon en les projetant sur la couche de la ligne médiane. Nous avons utilisé l'analyse des correspondances pour évaluer : 1) l'association des localisations individuelles des esturgeons avec trois secteurs de rivière : la rivière Gatineau, la rivière Désert et la rivière de l'Aigle et 2) l'association entre les localisations des esturgeons en fonction de deux groupes migrateurs distincts et les trois secteurs de rivière, par mois de l'année.

Basé sur les résultats de la seconde analyse des correspondances, toutes les localisations ont été classées selon deux états spatiaux : ceux dans la rivière Gatineau (état 1; où les habitats d'hivernage étaient situés) et ceux ailleurs (état 2). Pour déterminer si des variables environnementales étaient des prédicateurs potentiels des mouvements saisonniers des esturgeons entre ces deux états, nous avons utilisé un modèle de Markov de premier ordre à deux états avec covariables temporellement dépendantes, tel qu'implémenté dans le package *msm* dans R (R Development Core Team 2011). Les covariables utilisées dans le modèle étaient la température de l'air, le niveau de la rivière Gatineau en guise d'indicateur de la variation hydrologique dans l'habitat d'hivernage, et la photopériode. Le modèle de Markov quantifie l'influence des

covariables sur l'intensité des transitions entre les états, laquelle peut être liée à la probabilité de déplacements entre états sur une période donnée (Jackson 2011). Toutes les covariables étaient standardisées.

Résultats

Tous les poissons suivis ont passé l'hiver dans la rivière Gatineau, essentiellement à trois sites localisés entre les rkm 9 et 13; le site Deep Pool (rkm 9; Fig. 2.1) avait la plus grande concentration d'individus en hiver. Des graphiques de la position des individus suivis (rkm) en fonction du jour calendaire (Fig. 2.2) ont indiqué que les individus pouvaient être classés en deux catégories générales reflétant des différences dans les patrons de mouvements saisonniers. Premièrement, des migrateurs sur courte distance (Short-range migrants; SRM) passaient l'hiver dans la Gatineau nord (rkm < 13.12; Fig. 2.1), entraient subséquemment dans la rivière Désert et n'entraient pratiquement jamais dans la rivière de l'Aigle (Fig. 2.2). Deuxièmement, des migrateurs sur longue distance (Long-range migrants; LRM) passaient aussi l'hiver dans la rivière Gatineau nord, mais migraient chaque année dans la rivière de l'Aigle dans et au-delà de la section des rapides (rkm 68.85; Fig. 2.1) et, dans la plupart des cas, atteignaient la confluence avec la rivière Hibou pendant la transition hiver-printemps, y demeurant pour des périodes variant considérablement entre individus (cf. les individus 2 et 4; Fig. 2.2). La montaison printanière des LRM dans la rivière de l'Aigle était généralement rapide comparativement à la dévalaison automnale vers les aires d'hivernage, laquelle montrait plus de variabilité à la fois entre individus et entre les années pour un individu donné (Fig. 2.2). Les individus ayant été suivis pour plusieurs années affichaient généralement de la cohérence dans leurs patrons de migration saisonnière; soit ils montaient au-delà des rapides de la rivière de l'Aigle (LRM) ou ils demeuraient dans les rivières Désert et Gatineau (SRM) à chaque année.

L'ordination des localisations individuelles par l'analyse des correspondances (Fig. 2.3) a généré un arrangement clair des individus sur deux dimensions linéaires, chacune ancrée sur les sites d'hivernage collectifs de la rivière Gatineau et s'étendant de

là vers les sites utilisés le reste de l'année, soit de la rivière Désert (SRM) soit de la rivière de l'Aigle (LRM). L'ordination a procuré un argument additionnel pour assigner les individus aux catégories SRM et LRM.

L'ordination des localisations groupées par catégories de migrateur (Fig. 2.4) a procuré de l'information additionnelle sur la chronologie des migrations saisonnières pour les deux groupes. Des différences dans les patrons de migration saisonnière entre LRM et SRM ont mené des distributions fortement contrastantes de fréquence des localisations (SRM : unimodale; LRM : bimodale) (Fig. 2.5a) et dans les patrons globaux d'occupation spatiale (Fig. 2.5b). Les coefficients de régression partiels du modèle de mouvement markovien (Tableau 2.2) indiquaient que, pour les LRM, le mouvement printanier sortant de la rivière Gatineau (transition 1,2) était influencé par la photopériode, la température et le niveau de la rivière Gatineau; le retour dans la Gatineau à l'automne (transitions 2,1) était influencé par la photopériode et la température. Pour les LRM, le pic de la probabilité quotidienne de transition sortant de la rivière Gatineau a été estimé avoir lieu le 22 avril (Fig. 2.6). En harmonie avec la migration printanière rapide et la migration automnale plus graduelle décrite pour les LRM (Fig. 2.2), la différence entre les probabilités quotidiennes transitions amont et aval (la distance verticale entre les courbes lowess dans la figure 2.6, panneau de gauche) change abruptement au printemps et plus graduellement en automne. Les mouvements saisonniers des SRM semblaient être moins influencés par les covariables environnementales, néanmoins, semblables aux LRM, les mouvements printaniers semblaient être associés avec le niveau de la rivière Gatineau (Tableau 2.2). Pour les SRM, une légère augmentation des probabilités quotidiennes de transition hors de la rivière Gatineau (18 avril) coïncide pratiquement avec le pic des probabilités de transition 1,2 pour les LRM (Fig. 2.6).

Discussion

La redondance interannuelle des patrons de migration individuels et la réponse différentielle aux déclencheurs environnementaux par les deux types de migrateurs

apportent des preuves de l'occurrence de la migration partielle chez l'esturgeon jaune, et suggère que les comportements de mouvements individuels peuvent jouer un rôle important dans le maintien des structures de populations sur une période étendue.

Tous les individus utilisaient systématiquement des fosses profondes de la section amont de la rivière Gatineau comme site d'hivernage. Des déplacements hivernaux restreints ont aussi été documentés dans des études antérieures, où nous avons observé que des esturgeons se regroupaient dans des aires d'hivernage et demeuraient relativement sédentaires (p. ex., Rusak & Mosindy 1997; Borkholder *et al.* 2002). Dans la période printemps-été, les SMR élargissaient généralement leur utilisation de l'habitat pour inclure la section aval de la rivière Désert alors que les LRM migraient en amont sur environ 70 km jusqu'à des habitats d'eaux vives dans la rivière de l'Aigle, n'utilisant la rivière Désert que comme corridor de dispersion. Les différences de mouvements saisonniers entre SRM et LRM étaient cohérentes d'année en année. Puisque tous les esturgeons dans cette étude utilisaient simultanément certains secteurs, tels que les sites d'hivernage dans la rivière Gatineau, il est possible de conclure qu'ils avaient accès tous les mêmes habitats. Leur distribution dans l'aire d'étude résultait donc vraisemblablement de choix individuels (Johnson 1980; Manly *et al.* 2002).

La photopériode est vraisemblablement le meilleur indicateur de l'époque de l'année et son influence sur le réglage et le déclenchement de la migration et d'autres activités a été démontré chez plusieurs espèces de poissons, incluant des acipenseriformes (p. ex., Leggett 1977; McCormick *et al.* 1998; Oliveira & Sánchez-Vásquez 2010; Papoulias *et al.* 2011; Forsythe *et al.* 2012). La photopériode régule l'activité endocrine responsable pour les cycles circadiens et circannuels (Oliveira & Sánchez-Vásquez 2010) et peut servir de prédicateur de la phénologie des ressources (p. ex., la production primaire) et, conséquemment, de la disponibilité saisonnière dans des parcelles de ressources à distance (Bauer *et al.* 2011). La température influence aussi l'activité des poissons, incluant les mouvements migratoires et la reproduction (Rusak & Mosindy 1997; McCormick *et al.* 1998; Papoulias *et al.* 2011; Forsythe *et al.* 2012). La température a été proposée comme un important facteur environnemental régulant les

déclencheurs physiologiques pour diverses activités chez les poissons à l'intérieur d'une fenêtre temporelle procurée par la photopériode (McCormick *et al.* 1998). Dans la présente étude, les LRM étaient plus dépendants des indices environnementaux associés au temps que les SRM. Les LRM et SRM étaient vraisemblablement exposés à des conditions environnementales similaires dans les sites d'hivernage et sortaient de la rivière Gatineau avec passablement de synchronisme au printemps (*ca.* 3^{e} semaine d'avril; Fig. 2.6). Toutefois, le pic des probabilités de transitions hors de la rivière Gatineau était nettement plus haut pour les LRM que pour les SRM (Fig. 2.6) et la photopériode et la température apparaissaient seulement influencer les probabilités de transition pour les LRM (Tableau 2.2). Être au bon endroit au bon moment est vraisemblablement une tache plus difficile pour des organismes n'ayant pas d'information directe sur la disponibilité des ressources à des destinations potentielles éloignées. La dépendance à des signaux fiables indiquant la disponibilité des ressources (Bauer *et al.* 2011) devrait être plus forte pour les LRM que les SRM puisque le risque et le coût énergétique sont probablement beaucoup plus élevés pour ces premiers (Brodersen *et al.* 2008).

Contrairement aux probabilités de transition hors de l'habitat d'hivernage, lesquelles indiquaient une concentration de mouvement migratoire sur une courte période, il n'y avait pas de pic apparent pour les mouvements de retour vers les sites d'hivernage (Fig. 2.6). Les parcelles de ressources utilisées pour l'alimentation en été peuvent s'épuiser à différents moments dus à des différences d'échelle locale dans la production et la disponibilité des ressources, créant de l'hétérogénéité inter-parcelle quant au moment optimal pour quitter une parcelle (Van Moorter *et al.* 2009) et, conséquemment, dans la synchronisation interindividuelle du retour aux sites d'hivernage. Une telle hétérogénéité serait cohérente avec l'absence d'un pic bien défini dans les mouvements de retour à l'habitat d'hivernage des LRM. Au cours de l'été, les LRM utilisent des sites individualisés situés dans un éventail de distances des sites d'hivernage, une hétérogénéité spatiale pouvant aussi contribuer à étaler le moment de retour vers les sites d'hivernage.

Le niveau de la rivière Gatineau influençait la probabilité de transition de l'habitat d'hiver vers l'habitat d'été pour les LRM comme les SRM, mais n'avait pas d'influence détectable sur les probabilités de transition de l'habitat d'été vers l'habitat d'hiver (Tableau 2.2). L'influence de l'hydrologie des cours d'eau sur les mouvements des esturgeons semble varier d'un système à l'autre. Par exemple, dans le lac Black, Michigan, É.-U., un débit à la baisse ou à l'étiage stimulait l'entrée d'esturgeons jaunes dans un petit tributaire pour le frai, mais il n'y avait pas d'influence du débit sur les mouvements de retour au lac après le frai (Forsythe *et al.* 2012). Les déplacements en montaison d'esturgeons jaunes augmentaient avec l'augmentation du débit dans le système de la rivière Kettle, Minnesota, É.-U. (Borkholder *et al.* 2002) mais aucune influence du débit sur les migrations de frai n'a été trouvée dans le système de la rivière Rainy en Ontario, Canada (Rusak & Mosindy 1997). Ces différences de mouvement en réponse aux variations hydrologiques sont possiblement dues à des différences morphologiques locales des rivières et suggèrent que l'hydrologie est utilisée comme variable environnementale proximale pour évaluer le coût de la migration plutôt que pour prédire la disponibilité de la ressource. En accord avec cette notion, Auer (1999) suggère que la dévalaison rapide fréquemment observée après le frai chez les esturgeons pourrait être une stratégie pour éviter l'échouage alors que les niveaux d'eau déclinent rapidement dans l'habitat de frai après les crues printanières.

La nourriture, le refuge et le frai sont des motivateurs fondamentaux du comportement migratoire chez les poissons (Leggett 1977; Northcote 1978). L'esturgeon jaune fait typiquement preuve de déplacements restreints entre les habitats d'hivernage et d'alimentation (Fortin *et al.* 1993; Auer 1996; Wilson & McKinley 2004). Bien que des déplacements sur de grandes distances vers des habitats d'eaux vives peu profonds de petites rivières au printemps sont généralement attribuées aux migrations de frai (Auer 1996, 1999; Borkholder *et al.* 2002), les montaisons printanières des LRM ne faisaient preuve d'aucun lien clair avec des activités de frai. L'esturgeon jaune est un reproducteur polycyclique; les femelles frayent à intervalles de 4-9 ans et les mâles tous les 1-3 ans (Peterson *et al.* 2007); les individus prêts à frayer entreprennent des grandes migrations vers des sites de frai (Auer 1996) et ne demeurent

généralement pas longtemps dans la rivière de frai une fois le frai terminé (20 jours ou moins; Auer 1999; Bruch & Binkowski 2002). Pourtant, dans la présente étude, des LRM des deux sexes remontaient annuellement la rivière de l'Aigle à des sites de frai potentiels, où ils demeuraient pour le plus clair de l'été. Bien que la notion d'une disponibilité accrue des ressources dans l'habitat de destination (Leggett 1977; Brodersen *et al.* 2008) puisse procurer une explication partielle pour la montaison annuelle des LRM dans la rivière de l'Aigle, elle n'explique pas pourquoi les LRM migrent sur une distance de 70 km alors que les SRM demeurent dans un domaine vital beaucoup plus restreint.

Pour un large éventail de taxons animaux, le comportement de retour à des sites connus (angl. : homing) est associé à la mémoire à long terme (VanMoorter *et al.* 2009) laquelle peut être basée sur un ensemble complexe d'informations spatiales comprenant des indicateurs visuels, chimiques et olfactifs (Dodson 1988). Les esturgeons sont présumés retourner à leur rivière natale pour frayer (Auer 1999) et un fort instinct de homing (p. ex., fidélité à des sites de frai, d'alimentation et d'hivernage) a été documenté pour plusieurs espèces d'acipenseriformes (Vélez-Espino & Koops 2009).

Les expériences acquises en jeune âge ont le potentiel de définir les niches individuelles (Davis & Stamps 2004; Slagsvold & Wiebe 2007), ce qui peut mener à des utilisations spatiales différentielles au sein d'une population. Borkholder *et al.* (2002) ont observé que des esturgeons adultes suivis par télémétrie restreignaient leurs déplacements à une courte section de rivière en aval du site d'un ancien barrage. Ils ont conclu que le domaine vital de ces esturgeons pouvait découler d'expériences acquises préalablement au retrait du barrage (Borkholder *et al.* 2002). Similairement, les distributions contrastantes des SRM et LRM dans cette étude pourraient être le résultat d'une imprégnation différentielle de l'habitat en jeune âge et d'un homing subséquent.

Deux sites de frai sont connus de l'aire d'étude; un sous la chute Hibou et l'autre sous la chute Désert (Fig. 2.1). Les individus nés à ces deux sites pourraient être assujettis à une imprégnation différentielle de l'habitat; les larves dérivant du site de la

chute Hibou seraient imprégnées de la rivière de l'Aigle alors que ceux dérivant du site de la chute Désert seraient imprégnés de la rivière Désert (Auer & Baker 2002). L'imprégnation est supposée chez les esturgeons, et l'olfaction a été proposée comme mécanisme d'orientation principal menant le comportement de homing (Kasumyan 2002). Ainsi, le homing au site natal pourrait expliquer les vastes déplacements des LRM ainsi que les déplacements plus restreints des SRM. L'utilisation spatiale différentielle par les deux groupes augmente la probabilité d'un isolement reproductif (Hendry *et al.* 2000; Schluter 2001). À l'exception d'un individu SRM (poisson no. 8) ayant été observé sporadiquement dans la rivière de l'Aigle (Fig. 2.2), les individus suivis des deux groupes ne semblaient pas se mélanger aux sites de frai pendant la période du frai. Ainsi, les deux groupes pourraient faire preuve d'un isolement reproductif, et ce, possiblement en conséquence d'une imprégnation de l'habitat dans la première année de vie.

Nos résultats ont des implications en matière de gestion et de conservation. Premièrement, pour que les efforts de conservation et de gestion soient efficaces, la structure spatiale des populations concernées doit être adéquatement définie; si les deux groupes de la présente étude sont complètement ou partiellement isolés au plan reproductif, et si cet isolement est un produit d'imprégnation en bas âge, un déclin des effectifs dans une ou l'autre des unités pourrait ne pas être compensé par des immigrants de l'autre unité si l'utilisation spatiale est déterminée par une préférence aux sites natals plutôt que par la densité locale de population.

Deuxièmement, les migrations saisonnières avec des pics de mouvement très prévisibles rendent les esturgeons plus vulnérables à la capture aux moyens d'engins de pêche passifs, tels que des filets maillants. Troisièmement, les sites d'agrégation prévisibles rendent les esturgeons vulnérables au braconnage. Par contre, la prévisibilité des mouvements et sites d'agrégation peuvent aussi faciliter le suivi des populations et la surveillance de sites à risque élevé de braconnage. Quatrièmement, les migrations saisonnières de cette population englobent plusieurs types d'affectations territoriales et régimes de gestion (p. ex., agricultural, résidentiel, réserve autochtone, forêt privée,

terres fédérales et provinciales et zones d'exploitation contrôlée). Les stratégies de gestion doivent considérer un éventail correspondant des menaces et besoins, lesquels génèrent des défis de taille pour l'élaboration et l'implémentation de règlementations et stratégies de gestion locales. Cinquièmement, les stratégies actuelles pour la gestion, la conservation et le rétablissement de l'esturgeon jaune focalisent sur un cycle de vie associé à une croissance en milieux lacustre ou en grande rivière, avec des migrations vers des petites rivières essentiellement pour le frai (p. ex., Auer 1996; Dumont *et al.* 2011; Mailhot *et al.* 2011). Le cycle de vie des esturgeons de la présente étude est restreint à un environnement lotique, un contexte susceptible de nécessiter des stratégies de gestion alternatives.

Finalement, la fidélité aux aires de répartition saisonnières a des conséquences d'ordre écologiques et de conservation puisque si les animaux retournent toujours aux mêmes aires, la population dans son ensemble peut être incapable d'altérer ses patrons de migration quand l'habitat est perdu ou dégradé dans une ou plusieurs des ces aires (Morrison & Bolger 2012). Comprendre l'hétérogénéité des populations en termes de fidélité et des comportements migratoires est par conséquent nécessaire pour développer des plans de conservation efficaces pour faire face aux changements de l'habitat dans les aires saisonnières.

CHAPITRE II

INTRAPOPULATION VARIATION AND ENVIRONMENTAL DRIVERS OF SEASONAL MOVEMENT IN RIVER-DWELLING LAKE STURGEON

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Summary

1. Migration is a fundamental attribute of animal behaviour that can shape the fate of individuals, influence population dynamics and spatial use, and drive ecosystem-level interactions. Understanding the causes of migration can yield insight into the mechanisms underlying variation in population distribution and dynamics, and provide guidance for management and conservation.

2. Partial migration is considered to be the dominant form of migration in nature. The phenomenon is a consequence of individual decisions made to enhance fitness, where the decision process is subject to intrinsic and extrinsic influences.

3. We followed individual seasonal movements of 26 adult lake sturgeon (*Acipenser fulvescens*) in a stream and river network of southern Quebec, Canada. Lake sturgeons were tagged with internal radio transmitters between May 2006 and April 2010, and were tracked bi-weekly to monthly until late November 2010.

4. We used correspondence analyses to assess the distribution of individuals and the seasonal distribution of two distinct migrant groups among river sectors. To determine whether environmental variables (photoperiod, water level and temperature) were potential predictors of sturgeon seasonal migrations between winter and summer habitats, we used a two-state Markovian movement model with time-dependent covariates.

5. Individual movements were broadly consistent across years. All sturgeons could be classified into two distinct yearly migration patterns, characterized by a common, collective overwintering habitat, and either short- or long-range seasonal movements. Environmental variables appeared to drive seasonal movements but had a differential influence between the two migrant groups. The two groups did not mix at potential spawning sites during the spawning period.

6. The year-to-year consistency of individual migratory patterns and the differential response of the two migrant groups to potential environmental drivers provide evidence for the occurrence of partial migration in lake sturgeon, and suggest that individual movement behaviour can play an important role in maintaining population structure over an extended period of time. We hypothesise that partial migration in this population may result from early-age imprinting and subsequent homing to natal sites.

Keywords: *Acipenser fulvescens*; environmental effects; Markovian transition model; partial migration; population heterogeneity

Introduction

Movement is a fundamental attribute of animal behaviour that can shape the fate of individuals, influence population dynamics and structure, and drive ecosystem level interactions (Dingle & Drake, 2007; Chapman *et al.*, 2011b; Holdo *et al.*, 2011). Migration is the form of movement used by many animals to cope with changes in both their needs and the location of resources in time (Alerstam, Hedenström & Åkesson, 2003; Dingle & Drake, 2007; Beyer *et al.*, 2010); migrating to an alternate habitat ultimately increases fitness by offering access to needed resources (Leggett, 1977; Northcote, 1978; Alerstam *et al.*, 2003). However, migration also has costs and individuals must decide which strategy – move or stay put – offers the best tradeoffs between costs and benefits (Brodersen *et al.*, 2008). Because this decision is made individually, intrapopulation variation can lead to coexistence of resident and migratory individuals, a phenomenon known as partial migration (Jonsson & Jonsson, 1993; Kaitala, Kaitala & Lundberg, 1993; Chapman *et al.*, 2011a).

Partial migration is widespread across a variety of animal taxa and is considered to be the dominant form of migration in nature (Lundberg, 1988; Jonsson & Jonsson, 1993; White *et al.*, 2007; Chapman *et al.*, 2011a; Grayson, Bailey & Wilbur, 2011). In fish populations, partial migration is well documented in a variety of ecological contexts and at different spatial scales, e.g., migrations driven by seasonal predation-forage tradeoffs (Brodersen *et al.*, 2008), diel vertical migrations (Mehner & Kasprzak, 2011), alternative life history tactics (Kerr, Secor & Piccoli, 2009; Swanson *et al.*, 2010), and movement between breeding and overwintering habitat in monocyclic (i.e., which reproduce annually) species (Shaw & Levin, 2011). Partial migration in polycyclic species (in which some mature individuals typically do not reproduce every year, or skip years for various reasons; Rideout, Rose & Burton, 2005) has received comparatively less attention in the partial migration literature (Shaw & Levin, 2011; Chapman *et al.*, 2012b) even though it is a relatively common strategy in long-lived iteroparous fish (Rideout *et al.*, 2005). Given the diversity of forms partial migration can take and the array of ecological and evolutionary consequences that this diversity entails (Chapman *et al.*, 2011a, 2012b), examining movement patterns at the individual level can yield

insight on the mechanisms underpinning the phenomenon (Brodersen *et al.*, 2008; Kerr *et al.*, 2009). For individuals, migration includes two fundamental decision components: *when* and *where* to go (Bauer *et al.*, 2011). Both components are subject to extrinsic and intrinsic influences. First, to decide *when* to go, animals rely on sets of environmental and internal cues, the latter including developmental stage and physiological state (Trépanier, Rodríguez & Magnan, 1996; Hunter, Fox & Able, 2009; Bauer *et al.*, 2011); water temperature, stream discharge and photoperiod are proximate environmental cues that influence the initiation of migration in many fish species (e.g., Jonsson, 1991; Trépanier *et al.*, 1996; Rusak & Mosindy, 1997; Hunter *et al.*, 2009). Second, *where* to go can be influenced by genetics (Biebach, 1983), social learning (Dodson, 1988; Odling Smee & Braithwaite, 2003) and long-term memory (Davis & Stamps, 2004; Van Moorter *et al.*, 2009).

The lake sturgeon (*Acipenser fulvescens* Rafinesque) is a long-lived, polycyclic iteroparous species; males spawn every 1-3 years and females every 4-9 years (Peterson, Vecsei & Jennings, 2007). Mature individuals in a population, even within a single cohort, can be either migrating or non-migrating, owing to differences in individual and intersexual gamete maturation (Auer, 1996; Peterson *et al.*, 2007). Lake sturgeons can exhibit fidelity to sites used both for spawning (Auer, 1999; Forsythe *et al.*, 2012; Rusak & Mosindy, 1997; Welsh *et al.*, 2008) and non-spawning activities (Rusak & Mosindy, 1997; Knights *et al.*, 2002; Smith & King, 2005), and genetic studies on several species of sturgeon support the notion that individuals home to natal rivers (Stabile *et al.*, 1996; Smith *et al.*, 2002; Welsh *et al.*, 2008). Although spawning migrations can span several hundred kilometers (Auer, 1996), adult lake sturgeons are relatively sedentary at other times; movements within 10-14 km home ranges have been documented for many populations (Peterson *et al.*, 2007). Lake sturgeons are typically lacustrine or large-river dwellers and migrate to small to medium rivers only to spawn (Auer, 1996; Peterson *et al.*, 2007). Little is known about seasonal movements in lake sturgeon populations that reside year-round in streams and small rivers and do not have access to lacustrine or large-river habitats (but see Rusak & Mosindy, 1997; Borkholder *et al.*, 2002; Knights *et al.*, 2002).

In this study, we used active radio-telemetry to follow movements of adult lake sturgeons in a river network over a 5-year period. We describe intrapopulation variation in seasonal movements of lake sturgeon within the river network and investigate the role of time-dependent environmental variables (photoperiod, temperature, and river level) as potential drivers of migratory movements in this population.

Methods

Study area

The study area encompasses a heterogeneous network of streams and rivers centered on the Kitigan Zibi Anishinabeg Algonquin First Nation Reserve (KZA; N46°20' W75°58'), in the Gatineau River watershed alluvial plains, Quebec, Canada. The network comprises 7.24 km^2 (at low bank) of continuous riverine habitat accessible to adult lake sturgeon, extending over 106 river km of the Gatineau, Desert, and Eagle Rivers and short portions of Hibou River and Bitobi Creek (Fig. 2.1). The portion of the network under study is naturally bounded by landscape features such as falls, cascades, and steep rapids.

The Gatineau River (watershed area = 237 km^2; length = 386 km) is the largest river in the network; it is regulated monthly at the Mercier dam, located 25 km north of the St. Joseph Rapids (Fig. 2.1). From the St. Joseph Rapids (river km 0.00), the upper-Gatineau segment runs for 13.12 km before its confluence with the Desert River; several large pools (up to 30 m deep) in this segment provide primary overwintering grounds for lake sturgeon. The lower-Gatineau segment runs south to Tête-des-Six Rapids, 6.48 km downstream from the confluence of the Gatineau and Desert rivers.

The Eagle River flows 55.71 km north-east into the Desert River. Upstream of its confluence with the Hibou River, the Eagle River is meandering, highly entrenched, and has numerous small scour pools located in bends; Eagle Cascade impedes upstream passage of sturgeon beyond rkm 88.98 (Fig. 2.1). The portion of the Hibou River

accessible to sturgeon is 620 m in length; it is delimited upstream by an impassable fall (Hibou Falls; height > 3 m) and downstream by a deep confluence pool (Black Rollway Pool; depth > 9 m). Entrenchment declines progressively downstream from the confluence with the Hibou River; habitats include an assortment of a highly entrenched segment comprising riffles and rapids of various gradients (rkm 80.03 - 68.85; Fig. 2.1), followed by a more meandering segment characterized by lower gradient and shoal, lateral pool, and corner scour pool habitats. The portion of the Desert River that is accessible to sturgeon is delimited upstream by a steep fall (Desert Falls). Below its confluence with the Eagle River, the Desert River is characterized by alternating shoals and pools and is strewn with large woody debris. From the Desert River, sturgeon have access to an old meander (oxbow) of the Desert River, approximately 500 m in length and generally separated from Bitobi Creek by wood jams, debris and shallow depths.

Fish capture and radiotelemetry

A total of 26 adult lake sturgeons (total length 970-1460 mm) were captured on the Desert, Eagle and Hibou Rivers by means of gill nets (203-mm mesh) between May 2006 and April 2010 and tagged individually by surgical insertion of internal radio transmitters (model MCTF-3L; Lotek Engineering Systems, ON, Canada), following Ross & Kleiner (1982). Transmitters (73 x 16 mm; 26 g in air; 400 mm flexible antenna) had a battery life expectancy of 1001 days. Surgery was performed near the sites of capture. Before surgery, fish were anaesthetized (stage IV; Summerfelt & Smith, 1990) by submersion in a clove oil solution (60 mg l^{-1}; Peake, 1998), weighed, and measured (total and fork length). When possible, sex was determined by examination of the gonads during surgery. After surgery, fish were maintained under observation in large in-river holding pens (4 mm knotless nylon mesh netting) until they recovered from anaesthesia and were then released at their site of capture. The ratio of transmitter to fish weight was always below 2%, as recommended by Winter (1996). Postsurgical survival was 100% for the extent of the study.

Sturgeon movements were followed by radiotelemetry between May 2006 and November 2010 (receivers: SRX400 or Biotracker, Lotek Engineering Systems, Newmarket, ON, Canada; R410, Advanced Telemetry Systems Inc., Isanti, MN, USA; antenna: hand-held, three-element Yagi). Localizations were done by motor boat, or by canoe or by foot in areas that were inaccessible by motor boat. Radio transmitters were replaced on four occasions when their batteries died out (Table 2.1).

Between 16 May 2006 and 26 March 2010, telemetry surveys were conducted weekly (May-October) or every 15-30 days (November-April). No survey was conducted between 30 November 2008 and 5 May 2009, nor between 30 November 2009 and 25 February 2010. In 2010, surveys were conducted twice weekly from April to September and weekly in October and November. For each localization, geographic coordinates were recorded with a handheld GPS (GPSmap 76, Garmin, Olathe, Kansas, USA); depth and water temperature were measured using a sonar equipped with a temperature probe (GPSmap 420s, Garmin, Olathe, Kansas, USA). Precision of localizations was determined to be <3 m in field tests in the Desert River, in which a naive operator had to retrieve transmitters hidden at depths of 3-4 m (N = 13 tests).

Data analysis

Fish locations were plotted on a GIS layer to assess spatial distribution patterns within and across individuals. A river median line was traced on a GIS layer and calibrated in river kilometres (rkm) from the St. Joseph Rapids in the upper Gatineau River (rkm 0.00), the northernmost limit of the study area. Fish locations were assigned a rkm value by projecting them onto the river median line. We used correspondence analysis to examine: 1) the association of individual sturgeon locations with three river sectors: the Gatineau River, the Desert River and the Eagle River and 2) the association between locations of sturgeons in two migrant groups and the three river sectors, by month of the year. The first correspondence analysis was based on a 3 x 26 contingency matrix of location counts summed across months of the year and cross-classified by river

sector and tracked individual. The second analysis was based on a 3 x 48 contingency matrix of location counts cross-classified by river sector and month-migratory group combinations (group1-month1, ..., group1-month12, group2-month1, ..., group2-month 12), Correspondence analyses were performed using the *vegan* package in R (R Development Core Team 2011).

Based on the results of the second correspondence analysis, all locations were classified into two spatial states: those within the Gatineau River (state 1) and those elsewhere (state 2). To determine whether environmental variables were potential predictors of sturgeon seasonal migrations between these states, we used a two-state first-order Markov model with time-dependent covariates, as implemented in the *msm* package in R (R Development Core Team 2011). The environmental covariates used in the analysis were air temperature, photoperiod, and Gatineau River level (see below). The Markov model quantifies the influence of individual covariates on transition intensities between states, which in turn can be linked to the probability of shifts between states over a given time period (Jackson, 2011). Daily mean air temperature was recorded at a weather station 12.5 km south of the Desert-Gatineau River confluence (Environment Canada 71721 WMO ID; N46°16'29", W75°59'31"). Daily photoperiod was estimated from the Center for Biosystem Monitoring model (CBM) for 46.29° latitude and daylenght coefficient $p = 0.0°$ (Forsythe & Rykiel, 1995). Daily mean Gatineau River level (Hydro-Quebec hydrometric station no. 04801; N46°42'44", W75°59'1", 25 km upstream from St. Joseph Rapids) was used as an indicator of hydrological variation in the overwintering habitats. All covariates were standardized.

Results

All tracked fish overwintered in the upper Gatineau River, mostly at three sites located between rkm 9 and rkm 13; of these sites, Deep Pool (rkm 9; Fig. 2.1) had the greatest concentration of overwintering individuals. Plots of the position of tracked individuals (rkm) as a function of calendar day (Fig. 2.2) indicated that individuals could be grouped into two broad categories that reflected differences in seasonal movement

patterns. Short-range migrants (SRM) overwintered in the upper Gatineau river (rkm < 13.12; Fig. 2.1) and subsequently entered the Desert River and rarely ascended beyond the Eagle River rapids (rkm 68.85; Fig. 2.1), with the exception of individual 8, which was found sporadically in the rapids (Fig. 2.2). Long-range migrants (LRM) also overwintered in the upper Gatineau River, but migrated yearly into the Eagle River rapids and in most cases reached the confluence with the Hibou River during the winter-spring transition, remaining there for periods that varied considerably among individuals (cf. individuals 2 and 4; Fig. 2.2). The springtime ascent of LRM into the Eagle River was rapid relative to the autumnal descent back to overwintering sites, which showed greater variability both among individuals and among years for a given individual (Fig. 2.2). Individuals that were tracked for several years generally showed consistency in their pattern of seasonal migration and either ascended beyond the rapids (LRM) or remained in the Desert River (SRM) every year.

Ordination of individual locations by correspondence analysis (Fig. 2.3) yielded a neat arrangement of individuals along two linear dimensions, both "anchored" on the Gatineau River overwintering sites shared by SRM and LRM and extending from there either to the Desert River (SRM) or the Eagle River (LRM) sites used during the remainder of the year. The ordination provided a further means to assign individuals to the SRM (negative values along CA axis 1) or LRM (positive values along CA axis 1) categories.

Ordination of localizations grouped by migrant category (Fig. 2.4) provided additional information on the chronology of seasonal migrations for the two groups. Locations of LRM are strongly concentrated in the Eagle River during the period from May to July, whereas SRM are more evenly spread between the Desert River and the overwintering sites during the same period (Fig. 2.4). Differences in seasonal migration patterns between the LRM and SRM lead to markedly contrasting frequency distributions of locations (SRM: unimodal; LRM: bimodal) (Fig. 2.5a) and yearly patterns of spatial occupancy (Fig. 2.5b).

The partial regression coefficients from the Markovian movement model (Table 2.2) indicated that for LRM, springtime movement out of the Gatineau River (1,2 transitions) was influenced by photoperiod, temperature and level of the Gatineau River. Autumnal return movements into the Gatineau River (2,1 transitions) were influenced by photoperiod and air temperature. For LRM, the peak in daily probability of transition out of the Gatineau River was estimated to occur on April 22 (daily mean temperature = 6.7 °C; day length = 13.7 h) (Fig. 2.6). Congruent with the rapid springtime migration and more gradual autumnal migration described earlier for LRM (Fig. 2.2), the difference between daily probabilities of upstream and downstream transitions (vertical distance between lowess smooths in Fig 2.6, left panel) changes abruptly in spring and more gradually in autumn. Seasonal movements of SRM seemed to be less influenced by the environmental covariates but, similar to LRM, springtime movements appeared to be associated with the level of the Gatineau River (Table 2.2). For SRM, a small springtime increase in daily probabilities of upstream transitions (18 April) nearly coincide with the peak in upstream transition probabilities for LRM (Fig. 2.6).

Discussion

The year-to-year consistency of individual migratory patterns and the differential response of the two migrant groups to potential environmental drivers provide evidence for the occurrence of partial migration in lake sturgeon, and suggest that individual movement behaviour can play an important role in maintaining population structure over an extended period of time.

All individuals consistently used deep pools in the upper Gatineau as overwintering sites. Restricted range winter movements were also reported in previous studies, where sturgeons were found to aggregate in overwintering areas and remain relatively sedentary (e.g., Rusak & Mosindy, 1997; Borkholder *et al.*, 2002). In spring-summer, SMR generally expanded their habitat use to include the lower section of the Desert River whereas LRM migrated upstream approximately 70 km to shallow fast-

flowing habitats of the upper Eagle River, using the Desert River only as a dispersal corridor. Differences in seasonal movements of SRM and LRM were consistent across years. Because all sturgeons in this study used some areas simultaneously, such as the overwintering habitat in the upper Gatineau River, and thus had access to the same habitats, their distribution across the study area presumably resulted from individual choices (Johnson, 1980; Manly, Mcdonald & Thomas, 2002).

Photoperiod is likely the most reliable indicator of the time of the year and has been shown to be involved in the timing and triggering of migration and other activities in many fish species, including acipenseriforms (e.g., Leggett, 1977; McCormick *et al.*, 1998; Oliveira & Sánchez-Vásquez, 2010; Papoulias *et al.*, 2011; Forsythe *et al.*, 2012). Photoperiod regulates the endocrinal activity responsible for circadian and circannual cycles (Oliveira & Sánchez-Vásquez, 2010) and can serve as a predictor of resource phenology (e.g., primary production) and, consequently, of seasonal availability in resource patches afar (Bauer *et al.*, 2011). Temperature also influences fish activity, including migratory movements and reproduction (Rusak & Mosindy, 1997; McCormick *et al.*, 1998; Papoulias *et al.* 2011; Forsythe *et al.*, 2012). Temperature has been proposed as a proximate environmental factor regulating physiological triggers to various activities of fish within a seasonal window provided by photoperiod (McCormick *et al.*, 1998). In the present study, LRM were more dependent of time-related environmental cues than SRM. LRM and SRM were likely exposed to similar environmental conditions at the overwintering sites and appeared to move out of the Gatineau River in relative synchronicity in spring (*ca.* 3rd week of April; Fig. 2.6). However, the peak transition probability out of the Gatineau River was markedly higher for LRM than for SRM (Fig. 2.6), and photoperiod and temperature only appeared to influence transition probabilities for LRM (Table 2.2). Being at the right place at the right time is likely to be a more challenging task for organisms that do not have direct information about resource availability at distant potential destinations. Dependence on reliable cues that indicate resource availability (Bauer *et al.*, 2011) should be stronger for LRM than for SRM because the risk and energetic cost of migration are likely much greater for the former (Brodersen *et al.*, 2008).

Unlike transition probabilities out of the overwintering habitat, which reflected a concentration of migratory movements over a short period of time, there was no apparent peak for movements back to the overwintering sites (Fig. 2.6). Local resource patches used for foraging during the summer may become depleted at different times owing to small-scale differences in resource production and availability. These differences can create heterogeneity in the optimal timing for departure from patches (Van Moorter *et al.*, 2009) and, consequently, in individual timing of return to overwintering sites. Such temporal heterogeneity would be consistent with the absence of a well-defined peak in movement of LRM back to the overwintering habitat. During the summer, individual LRM use sites located at a broad range of distances from the overwintering sites, and this spatial heterogeneity may also contribute to spread out the timing of return movements to overwintering sites.

The level of the Gatineau River influenced the daily transition probabilities from winter to summer habitat for both SRM and LRM but had no detectable influence on transition probabilities from summer to winter habitat (Table 2.2). The influence of river hydrology on lake sturgeon movement seems to vary across systems. For example, in Black Lake, Michigan, U.S.A., declining or seasonally low discharge stimulated entry of lake sturgeon into a small tributary for spawning, but had no influence on return movements to the lake after spawning (Forsythe *et al.,* 2012). Upstream movement rates of lake sturgeon increased with increasing discharge in the Kettle River system, Minnesota, U.S.A. (Borkholder *et al.,* 2002), but discharge had no detectable influence on spawning migrations in the Lake of the Woods-Rainy River system, Ontario, Canada (Rusak & Mosindy, 1997). These differences in movement responses to hydrological variation suggest that hydrology is used by lake sturgeon as a proximate environmental variable to evaluate upstream migration costs rather than predict resource availability. Consistent with this notion, the rapid downstream movement commonly observed in lake sturgeons following spawning may be a strategy to avoid stranding as water levels in the spawning habitat quickly decline after spring floods (Auer, 1999).

Food, refuge, and spawning are fundamental motivators of migration behaviour in fish (Leggett, 1977; Northcote, 1978). Lake sturgeons typically show restricted movements between foraging and winter habitats (Fortin *et al.*, 1993; Auer, 1996; Wilson & Mckinley, 2004). Seasonal movement by adult lake sturgeon can be nondirectional and result in expansion and contraction of the home range, rather than actual migration (Rusak & Mosindy, 1997; Borkholder *et al.*, 2002). Although extensive upstream movements to shallow, fast-flowing waters of smaller rivers during the springtime are generally attributed to spawning migrations (Auer, 1996; Auer, 1999; Borkholder *et al.*, 2002), upstream springtime movements by LRM showed no clear link with spawning activity. Lake sturgeons are polycyclic spawners; females spawn every 4-9 years and males every 1-3 years (Peterson *et al.*, 2007). Ripe lake sturgeons undertake extensive migrations to spawning sites (Auer, 1996) and generally do not stay in the spawning river for long after spawning (20 days or less; Auer, 1999; Bruch & Binkowski, 2002). Yet, in this study, LRM of both sexes migrated yearly up the Eagle River to potential spawning habitats, where they remained for most of the summer. Although enhanced resource availability in the destination habitat (Leggett, 1977; Brodersen *et al.*, 2008) may provide a partial explanation for the yearly movements of LRM to the upper Eagle River, it fails to explain why LRM migrate over distances exceeding 70 km while SRM remain within a considerably more restricted home range.

Homing behaviour in a wide range of animal taxa is associated to long term reference memory (Van Moorter *et al.*, 2009) which, in fish, can be based on complex spatial information that includes visual, chemical and olfactory cues (Dodson, 1988). Acipenseriforms have acute chemosensory capabilities (Kasumyan, 2002; Miller, 2004). Sturgeons are believed to return to natal rivers to spawn (Auer, 1999), and strong homing behaviour (spawning, foraging and overwintering site fidelity) has been documented for several species of acipenseriforms (summarized in Vélez-Espino & Koops, 2009). Early-age experiences have the potential to define individual niches, including habitat preferences (Davis & Stamps, 2004) and foraging habits (Slagsvold & Wiebe, 2007), which can ultimately lead to differential spatial use within a population. Borkholder *et al.* (2002) reported that adult lake sturgeons tracked by telemetry

restricted their movements within a short reach below the former site of a dam which had been in place from 1908 to 1995. They suggested that the home range of these sturgeons may be the result of experience acquired prior to the dam removal (Borkholder *et al.*, 2002). The contrasting seasonal distributions of SRM and LRM in the present study may similarly be a result of differential early-age habitat imprinting and subsequent homing.

Two spawning sites are known to the study area; one below Hibou Falls and the other below Desert Falls (Fig. 2.1). Individuals spawned at these two sites could be subject to differential habitat imprinting; with larvae drifting downstream from the Hibou Falls site primarily imprinted by the Eagle River and larvae drifting from the Desert Falls site imprinted by the Desert River (Auer & Baker, 2002). Imprinting is believed to occur in sturgeons, and olfaction has been hypothesized as the main orientation mechanism driving homing behaviour, as well as intersexual communication and long-distance food detection (Kasumyan, 2002). Thus, homing to natal habitats may explain the extensive yearly migrations of LRM, as well as the more restricted distribution of SRM. Differential spatial use by groups within a population increases the likelihood of reproductive isolation between the groups (Hendry *et al.*, 2000; Schluter, 2001; Chapman *et al.,* 2012a). With the exception of one SRM individual (fish no. 8), which was found sporadically in the Eagle River in springs of 2006 and 2007 (Fig. 2.2), tracked individuals in the SRM and LRM groups did not appear to mix at spawning sites during the spawning period. Hence, the two migrant types may be reproductively isolated, possibly as a result of early-age imprinting.

Our results have conservation and management implications. First, in order to guide conservation or management strategies, population structure, including any form of sub-population or sub-units, should be adequately defined (Svedang *et al.*, 2010). If migrant groups are totally or partially reproductively isolated units, a numerical decline in either unit may not be compensated by immigrants from the other unit if spatial use is determined by preference for natal sites rather than by local population density.

Second, seasonal migrations with predictable movement peaks make sturgeons more vulnerable to passive fishing gear, such as gill nets, particularly in rivers that can be spanned by the gear; local authorities should consider this in planning surveillance strategies for the studied population and others thriving in similar systems. Third, predictable aggregation sites make sturgeons vulnerable to poaching. However, predictability of movement timing and aggregation sites also facilitates population monitoring and surveillance at sites with high risk of poaching. Fourth, yearly seasonal migrations can encompass many land types and management regimes (e.g., agricultural, residential, aboriginal reservation, private forest, provincial and federal lands, and controlled harvesting zones). Management strategies must consider a correspondingly wide range of threats and needs, which creates challenges for the design and implementation of local regulations and management guidelines. Fifth, current strategies for management, conservation, and recovery of lake sturgeon focus on a life cycle associated with foraging and growth in lakes or large rivers, with migrations to smaller rivers mainly for spawning (e.g., Auer, 1996; Dumont *et al.*, 2011; Mailhot, Dumont & Vachon, 2011). The life cycle of lake sturgeon in the present study is restricted to a small riverine environment, which likely calls for alternative management strategies.

Finally, fidelity to seasonal ranges has ecological and conservation consequences because if animals always return to the same ranges, the population as a whole may be unable to alter their migration patterns when habitat is lost or degraded in one or more of the ranges (Morrison & Bolger, 2012). Understanding population heterogeneity in fidelity and migratory behaviour is therefore necessary to develop effective conservation plans for coping with habitat changes to seasonal ranges.

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Table 2.1. Individual fish data. n.d.: not determined; LRM: long-range migrant; SRM: short-range migrant.

Fish number	First location	Last location	Number of relocations	Sex	Total length (mm)	Weight (g)	Migrant class
1†	16-05-2006	25-11-2010	177	n.d.	1270	929	LRM
2	16-05-2006	17-11-2009	117	M	1080	630	LRM
3	17-05-2006	24-10-2008	73	M	1010	820	LRM
4	18-05-2006	17-11-2009	114	n.d.	1240	980	LRM
5	19-05-2006	16-10-2009	52	M	1390	1110	LRM
6†	19-05-2006	25-11-2010	166	F	1090	521	LRM
7	13-06-2006	31-10-2008	91	M	1030	591	LRM
8	13-06-2006	31-10-2008	72	n.d.	1100	722	SRM
9	14-06-2006	31-10-2008	90	n.d.	1205	970	LRM
10	01-08-2006	05-10-2009	92	n.d.	1220	1021	LRM
11	02-08-2006	16-10-2009	100	n.d.	975	592	LRM
12†	02-08-2006	25-11-2010	154	F	1090	672	LRM
13	04-08-2006	08-10-2008	75	n.d.	1290	1200	LRM

Table 2.1 (continued)

14	02-05-2007	17-11-2009	86	n.d.	1110	720	SRM
15	01-05-2007	18-11-2010	102	F	1460	1256	SRM
16	02-05-2007	01-11-2010	135	F	1210	906	SRM
17[†]	03-05-2007	25-11-2010	143	n.d.	1340	1350	SRM
18	28-05-2007	25-11-2010	122	F	1060	630	SRM
19	28-05-2008	25-11-2010	102	n.d.	1025	540	SRM
20	28-05-2008	14-09-2010	94	n.d.	1050	784	SRM
21	23-07-2009	25-11-2010	68	n.d.	1170	972	LRM
22	17-07-2009	25-11-2010	67	n.d.	1110	712	LRM
23	30-04-2010	25-11-2010	47	n.d.	970	370	SRM
24	30-04-2010	25-11-2010	46	F	1105	662	LRM
25	14-05-2010	25-11-2010	39	F	1190	1034	SRM
26	21-05-2010	25-11-2010	39	M	1340	1212	SRM

[†] Transmitters replaced in 2009 or 2010.

Table 2.2. Odds ratios derived from the Markovian movement model for effects of photoperiod, air temperature, and level of Gatineau River on daily state transition intensities, by migrant type. Transition codes represent movements out of the Gatineau River (1,2) or into the Gatineau River (2,1). Coefficient values greater than 1 indicate a positive effect of an environmental variable on the transition intensity; values smaller than 1 indicate a negative effect. LRM: long-range migrants, SRM: short-range migrants. Significant odds ratios are in bold.

Migrant type	Transition	Photoperiod		Air temperature		River level	
		Odds ratio	95% C.I.	Odds ratio	95% C.I.	Odds ratio	95% C.I.
LRM	1,2	**2.187**	1.438-3.325	**0.660**	0.492-0.885	**0.374**	0.281-0.498
	2,1	**0.318**	0.218-0.462	**2.554**	1.566-4.166	0.841	0.643-1.100
SRM	1,2	1.234	0.748-2.036	0.844	0.532-1.338	**0.519**	0.341-0.790
	2,1	0.638	0.402-1.012	1.142	0.694-1.877	1.056	0.770-1.447

Figure legends

Figure 2.1. Map of the study area showing the Eagle, Desert, and Gatineau Rivers and their tributaries. Arrows indicate the direction of flow. Distances (river kilometres; rkm) from St. Joseph Rapids are shown also.

Figure 2.2. Individual locations (rkm) of short-range (SRM) and long-range (LRM) migrants as a function of date; all years pooled. Horizontal dotted lines mark the downstream extremity of the rapids section in Eagle River (rkm 63.85) and the confluence of the Desert and Gatineau Rivers (rkm 13.12). The vertical dotted line corresponds to the peak in movements out of the Gatineau River (transition intensity; Fig. 2.6) for SRM (18 April) and LRM (20 April). Numbers identifying individual fish (see Table 2.1) are given above the plots.

Figure 2.3. Correspondence analysis (CA) ordination based on locations of individual fish (identified by number; see Table 2.1), for all months combined, in three river sectors. Symbols code for short-range (SRM; solid circles) and long-range (LRM; open squares) migrants.

Figure 2.4. Correspondence analysis (CA) ordination of locations of short-range (SRM, all individuals combined; solid circles) and long-range (LRM, all individuals combined; open squares) migrants, grouped by month, in three river sectors. Months are numbered sequentially starting with January. Symbols were slightly displaced at random ("jitter") to improve visibility.

Figure 2.5. a) Frequency distribution of fish locations (rkm; all years pooled) showing contrasting unimodal (short-range migrants; SRM) and bimodal (long-range migrants; LRM) distributions. b) Map of locations for SRM and LRM groups (all years combined), showing common use of the Gatineau and Desert Rivers by the two groups and nearly-exclusive use of the Eagle River (rkm > 33.85) by the LRM group. Locations were slightly displaced at random ("jitter") to improve visibility.

Figure 2.6. Daily transition probabilities estimated from the two-state Markov model for short-range (SRM) and long-range (LRM) migrants. Separate lowess smooth curves are shown for transitions out of the Gatineau River (black curves; filled circles) and into the Gatineau River (gray curves; open circles). Peak transition rates out of the Gatineau River are indicated by vertical dotted lines.

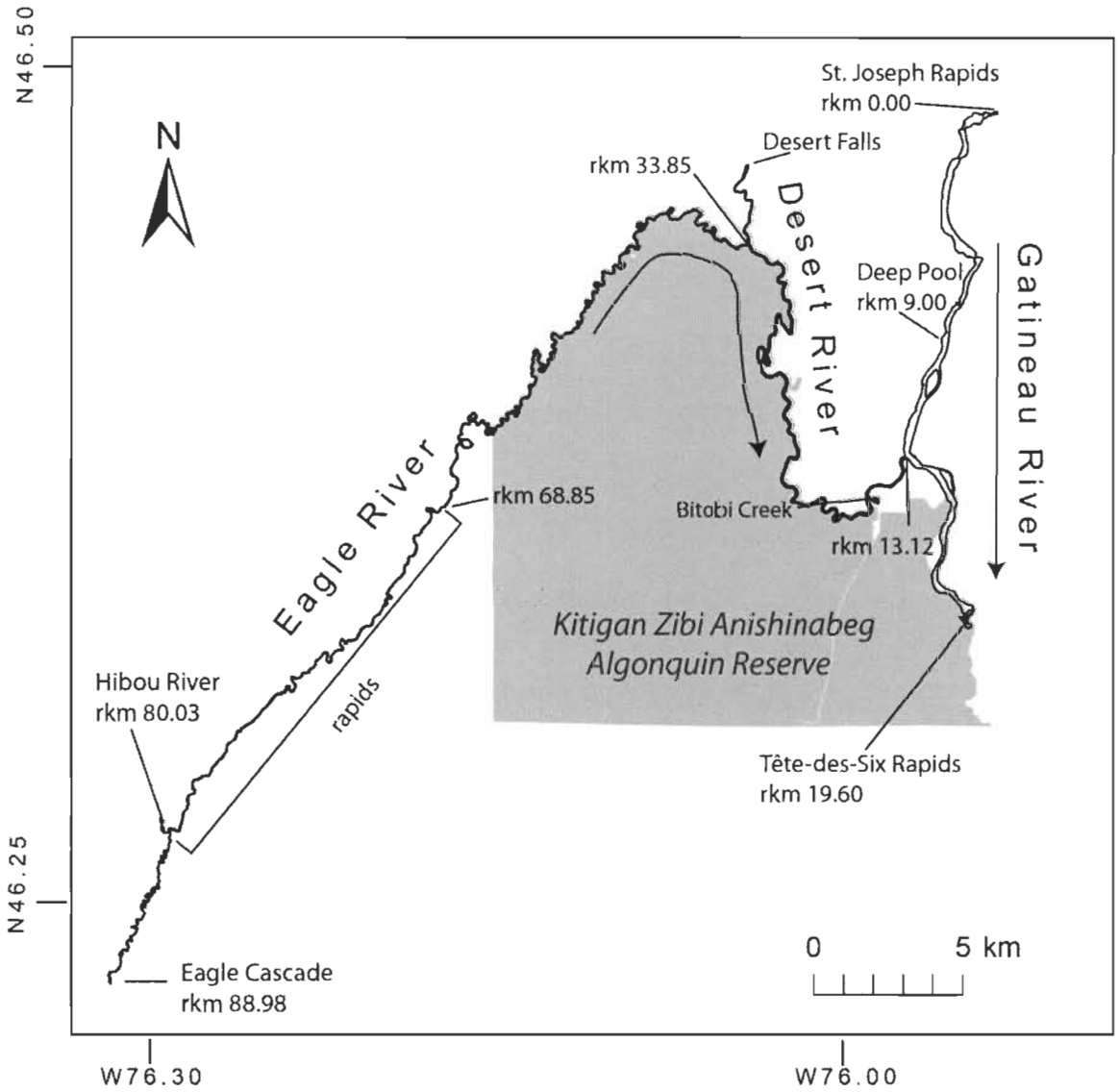

Figure 2.1. Déry & Rodríguez

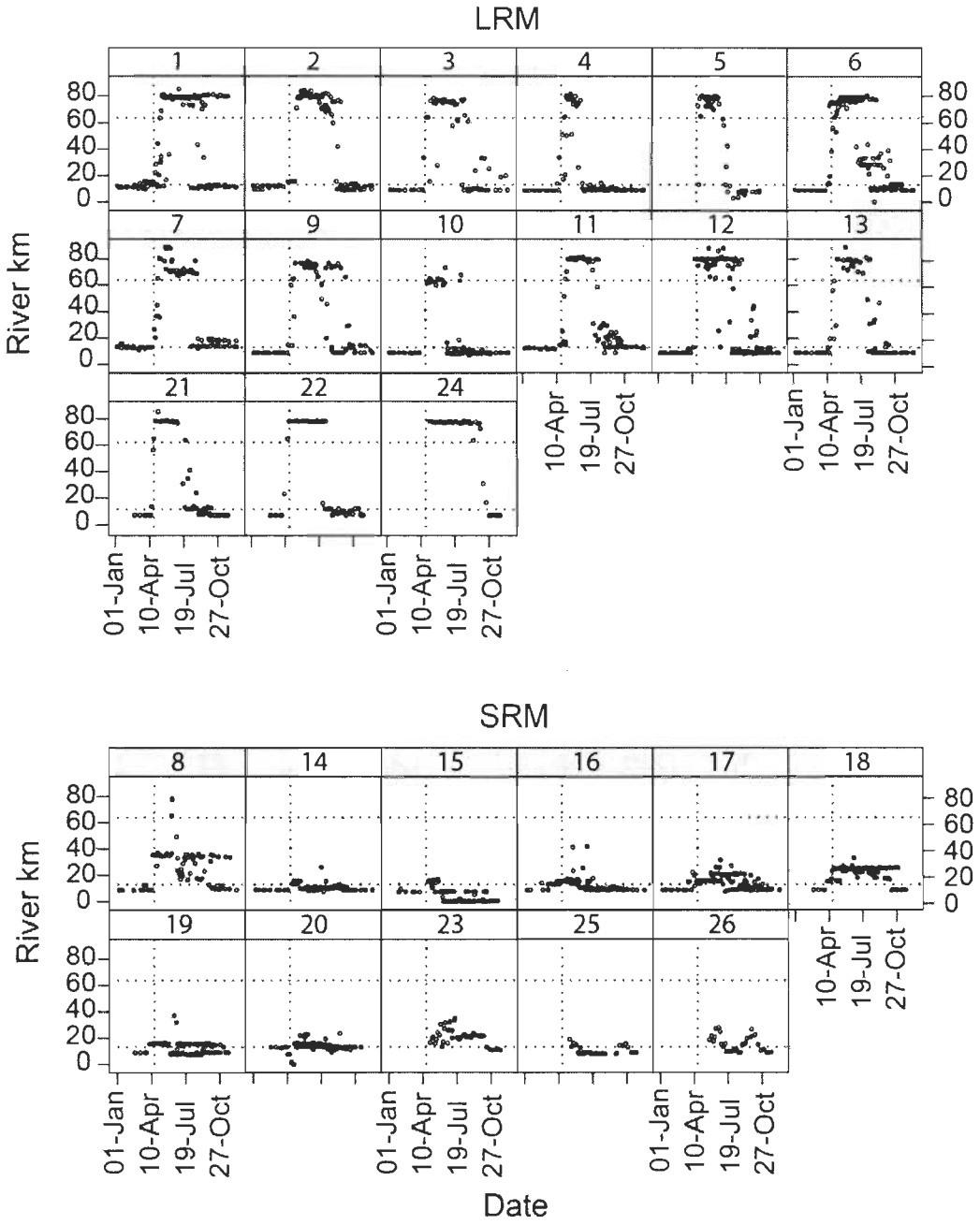

Figure 2.2. Déry & Rodríguez

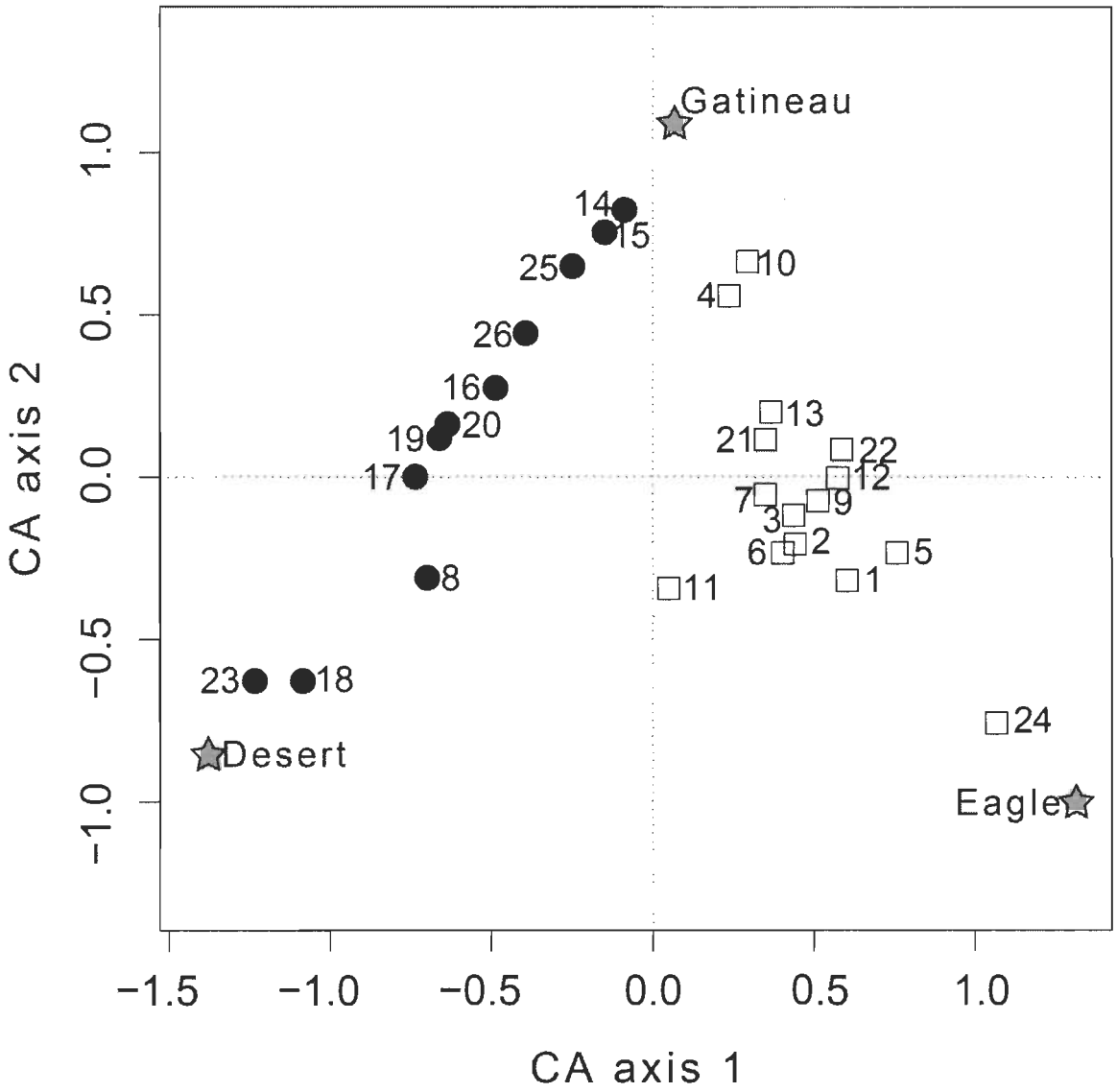

Figure 2.3. Déry & Rodríguez

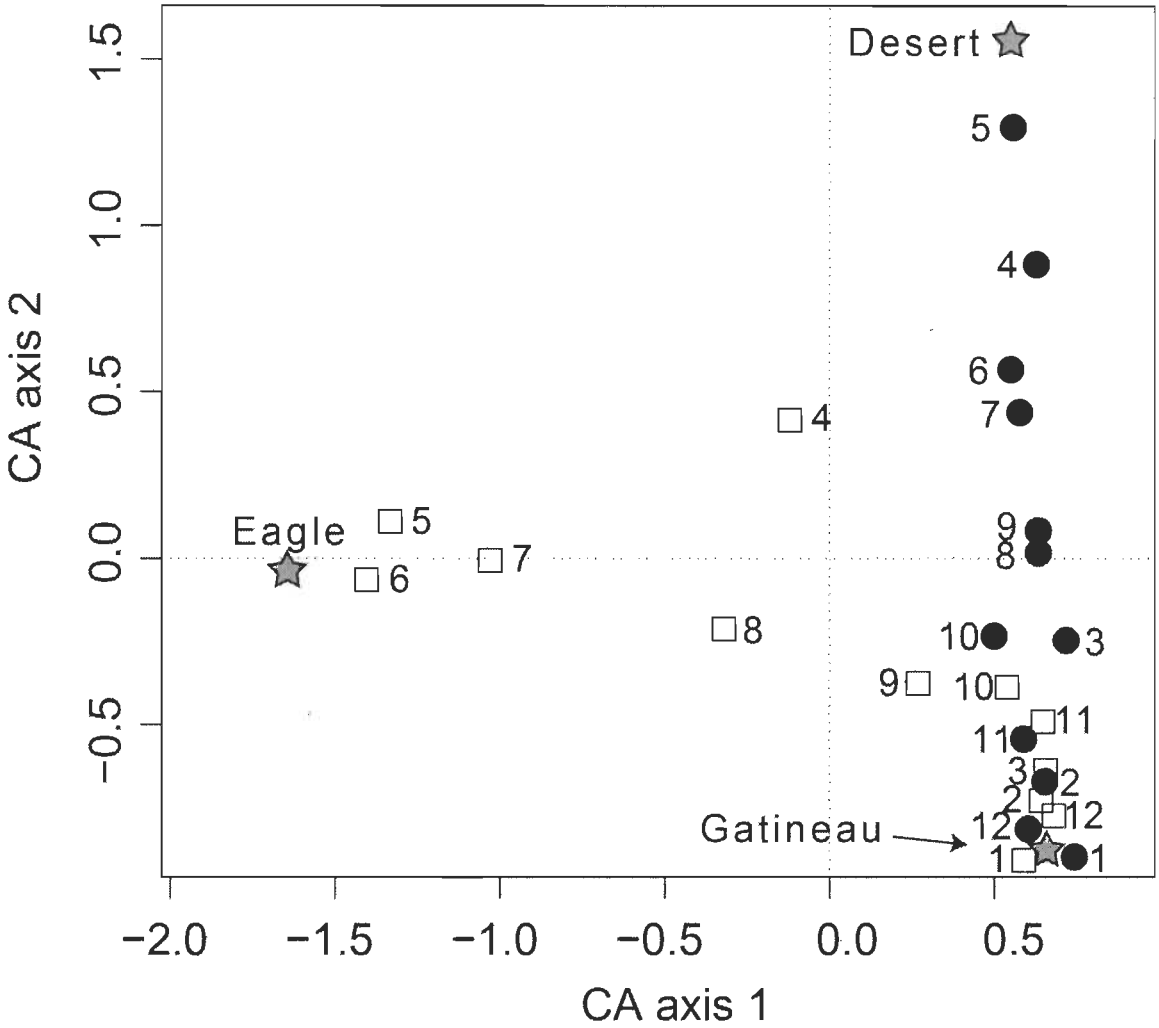

Figure 2.4. Déry & Rodríguez

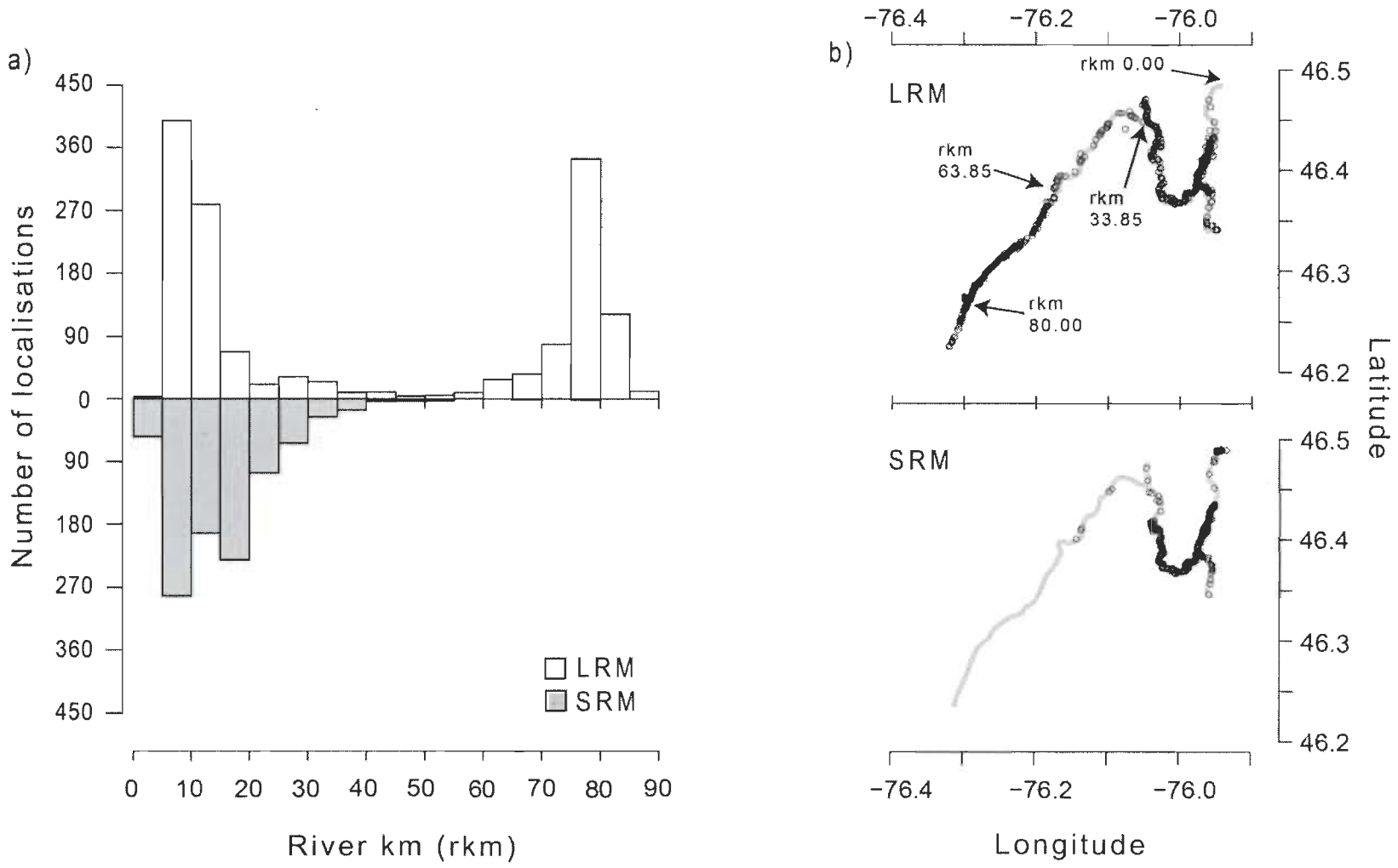

Figure 2.5. Déry & Rodríguez

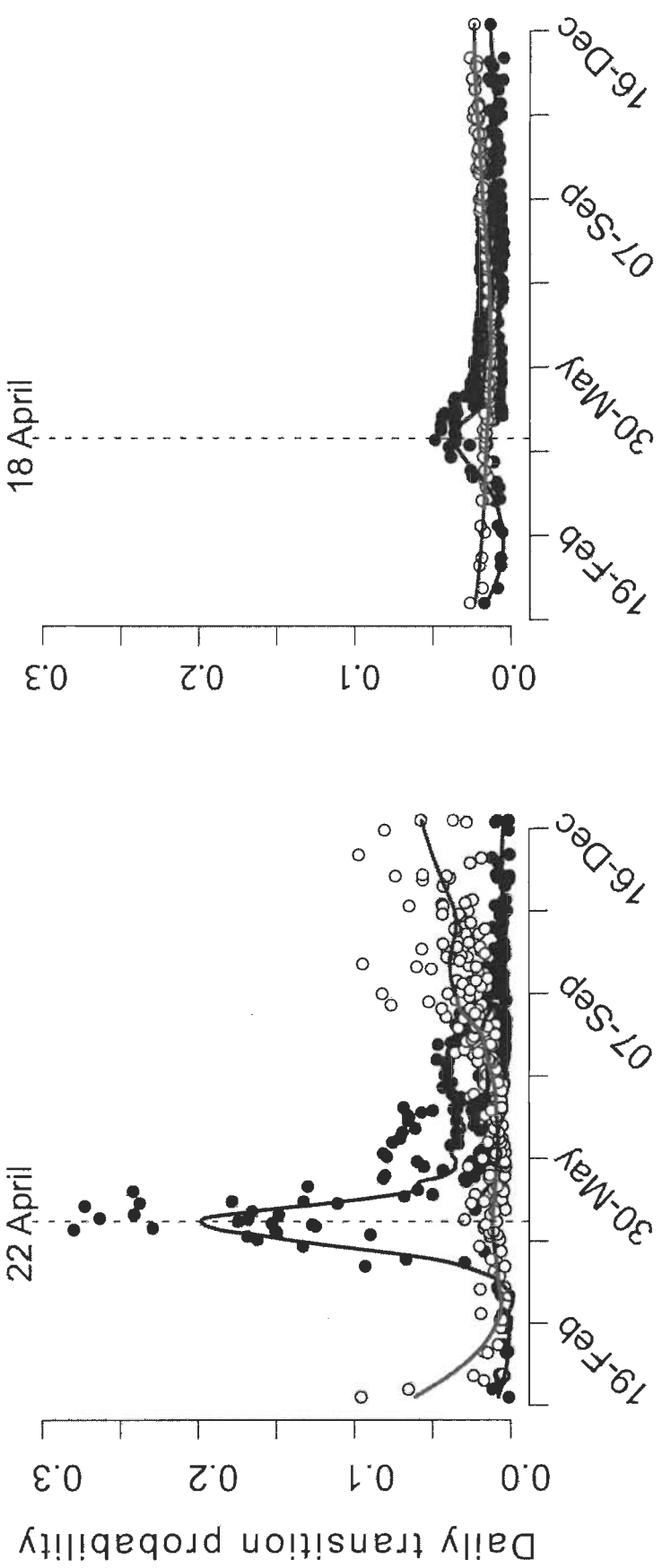

Figure 2.6. Déry & Rodríguez

ANNEXE

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